

CHEMICAL DEFENSE AND MAMMALIAN HERBIVORES

Bruce A. Kimball,

USDA/WS/National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521 and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523.

Frederick D. Provenza,

Utah State University, Department of Forest, Range, and Wildlife Sciences, Logan, UT 84322-5230.

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Contents

1. Plant Metabolism
2. Phytochemical Variation in Plants
3. Plant Defense Theory
4. Mammalian Metabolism of Phytochemicals
5. Mammalian Herbivory

Related Chapters

Glossary

Bibliography

Biographical Sketch

Summary

Herbivory is the interplay of plant form and function, herbivore anatomy and physiology, and foraging behavior. At the center of this interaction are the products of plant metabolism. Plants are producers of chemicals that can be classified as either primary or secondary metabolites. Primary metabolites are responsible for plant growth and also provide the nutrients mammals seek. Secondary metabolites are plant chemicals that, in part, defend plants against herbivores (toxins and antifeedants), pathogens (phytoalexins), and competing plants (allelochemicals). Chemical defenses deter mammalian herbivores by adversely influencing the physiology of the consumer. Defensive compounds vary not only among plant species, but also in space and time within individual plants. Herbivores may also influence how secondary metabolites are distributed in plants.

At the same time, herbivores have evolved both physiological and behavioral traits to circumvent plant defenses. Physiologically, herbivores are equipped with metabolic pathways designed to detoxify and eliminate defensive compounds. Behaviorally, herbivores "spread the risk" of consuming a toxic diet by eating a variety of foods (generalists) or focus their foraging efforts on a single plant species (specialists). Food mixing may also nutritionally guarantee that the herbivore can detoxify defensive compounds. However, neither the herbivores nor the plants have gained the advantage in this evolutionary arms race. Rather, evolutionary feedbacks have prevented both plants and herbivores from gaining the upper hand.

Plant chemicals (phytochemicals) contribute to the flavor of a plant as well as impact the well-being of the herbivores that ingest them. Both primary and secondary metabolites must be considered when assessing herbivory. Mammalian herbivores learn about the foods they eat from the interplay of phytochemicals and the physiological effects they produce. Learning produces aversions and preferences for other attributes of the food (what a food smells, looks, or feels like; where it may be found; who else eats it).

Both chemical defense allocation by plants and herbivory by mammals are dynamic, adaptive processes. Plants are capable of adapting to changing environmental conditions and herbivory. Herbivores are similarly equipped to recognize phytochemicals in the foods they eat and respond accordingly. These responses, both physiological and behavioral, permit mammalian herbivores to forage efficiently in the diverse and ever-changing phytochemical world they inhabit.

1. Plant Metabolism



1.1. Primary Metabolism

The universal constituents of plant cells and tissues are known as primary plant metabolites. They are the primary products of plant growth and the targets of foraging mammals. Examples include simple carbohydrates (e.g. glucose, sucrose), starches (e.g. amylose, amylopectin), lipids (e.g. triacylglycerol), and proteins (e.g. globulins). Carbohydrates are the principle products of photosynthesis. Most of the carbon dioxide fixed by plants is initially transformed into sucrose, the main storage sugar in plants. Sucrose can be easily broken-down into its component sugars via enzymatic hydrolysis. The plant enzyme invertase converts one molecule of sucrose into a molecule of glucose and a molecule of fructose. Cellulose (a polymer comprised of repeating glucose molecules) is the most abundant plant polysaccharide, providing the framework of plant cell walls.

Starch, a mixture of amylose (a linear molecule of 600 - 3,000 glucose units) and amylopectin (a branched molecule of 6,000 - 60,000 glucose units) is the pre-eminent source of stored carbohydrates in plants. A variety of starch-degrading enzymes are available in plants to produce any number of smaller oligosaccharides, maltose, and glucose directly from starch.

Lipids serve many functions in plants, including formation of cell membranes and exterior cuticle surfaces of aerial tissues. Triacylglycerol, three long-chain fatty acids attached to a glycerol molecule, is a prime form of carbon storage in seeds and a major source of calories for herbivores. Lipids may be enzymatically oxidized to yield free fatty acids for energy and sugar production.

Proteins are a source of nitrogen storage and account for a substantial portion of the dry weight of plants. Proteins and peptides are composed of amino acid building blocks, which lead to the great diversity in protein size and function. The numerous plant enzymes responsible for biochemical functions such as synthesis and metabolism of starch and lipids are also proteins.

1.2 Secondary Metabolism

Secondary plant metabolites differ from primary metabolites in that they do not contribute directly to plant growth and are not distributed universally in plant tissues. These metabolites take on many roles in plants, including serving as visual and olfactory cues for pollinators and seed dispersers. However, the most prominent role of secondary metabolites is defending plant tissues against herbivores, pathogens, and competing plants. The types and amounts of chemical defenses are often regulated by the plant and may be predicted. Chemical defenses against mammalian herbivores can be classified as either toxins or antifeedants. Toxins are normally present in relatively low concentrations in plants and extremely poisonous. Conversely, antifeedants are typically present in large quantities and not highly toxic to herbivores.

Monoterpenes and phenolics are the most common antifeedants in plants. Numerous vascular plants employ monoterpenes and phenolics to minimize mammalian herbivory on above-ground structures. Monoterpenes are the simplest volatile terpenes found in conifers, mints, composites, and citrus. They serve as toxins, oviposition stimulants, and feeding deterrents for insects. However, mammalian avoidance of many plants has also been linked to the antifeedant qualities of monoterpenes. Monoterpenes can be toxic in high doses, though mammals have sophisticated mechanisms to detoxify them. In toxic doses, monoterpenes inhibit acetylcholinesterase activity in mammals. In conifers, monoterpenes are present in high concentrations in the foliage and the vascular tissues.

Phenolics are a broad category of secondary metabolites that include tannins, lignins, and flavonoids. Tannins are found in the sap of living cells, in plant resins, and in plant and are classified as condensed or hydrolyzable. Condensed tannins are complex molecules consisting of repeating units of smaller phenols. Condensed tannins are not easily reduced into the smaller building blocks. Conversely, hydrolyzable tannins are readily broken down to the basic structural unit via acid, base, or enzymatic hydrolysis.

Tannins deter herbivores by inhibiting digestion and may also be toxic in large quantities. Mammalian plant avoidance has been correlated with tannin content for numerous plant species. Digestibility is inhibited when tannins form complexes with soluble plant proteins and carbohydrates as well as with mammalian digestive enzymes. Tannins are also known to impart astringency when ingested, however it is probable that astringency per se does not deter feeding. Rather, mammals may rely on learning processes to associate the sensation of astringency with inhibited digestibility.

Lignins are polymeric phenolics of high molecular weight that contribute rigidity to cell walls and internal structures of erect plants. Lignins deter herbivory via increased toughness of plant tissues and decreased digestibility (i.e. a physical defensive mechanism). Thorns, spikes, and hairs (trichomes) are examples of other physical defenses of plants. These structures can discourage sampling and decrease intake rates of plant tissues by both vertebrate and invertebrate herbivores. In general, physical defenses are most common in dry ecosystems and in regions of high herbivore densities.

Flavonoids, another class of phenolics, are important pigments contributing to flower, fruit, and leaf color. While most flavonoids are considered non-toxic, some such as rotenone are

highly toxic. Flavonoids are just one of many plant toxins that in small concentrations may deter herbivory. Other toxins include cardenolides (present in milkweeds), glucosinolates (mustards), furanocoumarins (parsnip), cyanogenic glycosides (legumes, sorghum), saponins (snakeweeds), and alkaloids (numerous herbaceous and woody plants).

Like alkaloids or cardenolides, many sesquiterpenes (the largest class of terpenoids) are also extremely poisonous and would be considered toxins rather than antifeedants. Sesquiterpenes are extensively variable in chemical structure and toxic to both insects and mammals. Herbaceous plants such as bitterweeds (*Hymenoxys spp*) and sneezeweeds (*Helenium spp*) contain sesquiterpene lactones that bind to sulfur-containing essential amino acids. As compared to monoterpene antifeedants, sesquiterpene lactones are toxic in much smaller doses. For example, the oral dose of α -pinene (a monoterpene common in conifers) required to produce mortality in fifty percent of rats tested (LD50) is 3700 mg/Kg, whereas the LD50 for helenalin (a sesquiterpene lactone found in sneezeweed) is 150 mg/Kg.

The metabolic effects of these toxins vary among herbivores. The plant itself is the first source of variation. The concentration of toxins may vary from tissue to tissue and over time. Among mammals, detoxification processes allow herbivores to tolerate certain levels of these phytochemicals. The herbivores ability to tolerate specific toxins is determined by dose, mode of action, metabolism, and nutritional state.

2. Phytochemical Variation in Plants



2.1 Variation within a Population

Just as plant morphology differs among plant species, so too do phytochemical constituents. The heritability of phytochemicals has been extensively studied in many plants, particularly monoterpenes in conifers. The pattern of terpene allocation in conifers may be controlled by only a few genes. Importantly, preferences of mammalian herbivores for certain plant genotypes and hybrids have been attributed to heritable defensive chemicals. In general, genetics dictate which phytochemicals are present while environment influences their relative abundances. However, patterns of defense allocation in response to the environment are scattered and difficult to predict. For example, mineral and water stress in conifers causes the concentrations of some monoterpenes to increase, while others decrease or are unaffected.

Biotic pressures also exert themselves on the expression of phytochemicals present in plants. The adaptive response of one species in response to the genetic changes of another is termed coevolution. Diffuse coevolution describes a system in which groups of populations evolve in response to genetic changes in each other. In order to affect a response, a population must exert a strong selective pressure. Because mammals are typically generalist herbivores, they probably have not played much of a role in coevolution of plant defenses. Interactions between plants and a variety of competitors, pathogens, abiotic factors, and insect herbivores likely have led to much of the phytochemical diversity observed today. However, mammals must deal with the suite of defenses arising in plants, regardless of the driving force.

2.2 Variation within an Organism

In addition to variation among species, the types and abundances of phytochemicals also vary within an individual plant. Because different plant tissues perform different functions, it is expected that secondary metabolites would vary among plant parts. For example, phytochemicals present in reproductive tissues that attract pollinators would not be necessary in the roots. The transportation systems of vascular plants allow phytochemicals to be translocated to specific organs. Concentration gradients have often been observed for many phytochemicals. For example, many plants exhibit great variation in terpene concentration among leaves, roots, stems, and reproductive parts.

Phytochemicals also vary temporally within plants. Seasonal changes in foliage phytochemistry are common. Maturation of Douglas-fir foliage includes increased concentrations of many terpene compounds. This trend of higher terpene concentration in older tissues is common in other organs such as stems and roots. Though temporal variation is usually considered in the context of seasonal or maturation effects, it is not limited to large-scale variation. Phytochemical variation can occur on an hourly scale. For example, diurnal variability of plant carbohydrates occurs because the rate of photosynthate export does not equal the rate of photosynthesis over the entire photoperiod. Such variation is significant and can be detected by foraging herbivores.

Direct changes in the distribution or abundance of plant defenses resulting from herbivory or environmental stress are termed induced responses. Induction allows plants to produce costly defenses only when they are needed. For example, mammalian herbivory can cause plants to increase the abundance of chemical defenses in new growth.

3. Plant Defense Theory



Plant defense theory attempts to describe how phytochemicals are allocated and distributed among plant species and within individual plants. The aim of these theories is to synthesize what is known about phytochemical defenses in a manner that makes useful predictions about the types of defenses a plant will employ to deter herbivory. It is an enticing area of research because patterns of phytochemical distribution are frequently observed.

The first theory attempting to explain patterns of chemical defenses was Plant Apparency Theory (PAT). In Apparency Theory, plants are characterized as being distributed in a landscape either unavoidably (apparent) or erratically (unapparent). In addition, PAT also considers individual plant tissues to be apparent or unapparent. Plants (or plant tissues) may be considered apparent (or unapparent) in both space and time. For example, seeds (fruit) would be considered unapparent in time because they are not present at all life stages of the plant.

Apparency theory predicts that apparent and unapparent plants will be defended differently because there is a trade-off between a plant's ability to escape herbivory and its ability to defend itself. Apparent plants employ "quantitative" defenses - dose dependent antifeedants such as monoterpenes or tannins. Quantitative defenses are considered to be costly to produce because they are required in large quantities. Conversely, unapparent plants rely on "qualitative" defenses toxins such as alkaloids and cardenolides that are lethal in small concentrations. Qualitative defenses are considered less costly to produce than quantitative

defenses, though there is evidence to the contrary.

Apparency theory predicts that long-lived plants are temporally apparent and would be highly defended by quantitative defenses. Thus, the deployment of monoterpene defenses in conifer foliage is predicted by plant apparency theory. Likewise, herbaceous annual plants are predicted to employ qualitative defenses because their tissues are unapparent in time. However, the observation that many apparent plant species are not chemically defended caused apparency theory to fall out of favor.

Optimal Defense Theory (ODT) provides an evolutionary view of plant defense. Two hypotheses are paramount to ODT: 1) organisms evolve defenses in a manner that maximizes individual fitness, and 2) defenses are costly. Optimal defense theory also recognizes the dynamic nature of chemical defense. Defenses are predicted to be allocated to plant tissues according to the value (as measured by individual fitness) to the plant. Further, defenses are predicted to be increased when the plant is subjected to attack and reduced when herbivores are absent. In ODT the cost of defense is measured against the loss of fitness resulting from herbivory.

The observation that slow-growing species were better defended than fast-growing ones led directly to the Resource Availability Hypothesis (RAH). The prediction that plant species in resource-poor environments favor production of chemical defenses is a paramount prediction of RAH. As with the majority of plant defense theories, RAH considers the costs of chemical defenses to be in a trade-off with plant growth. The production of defenses is favored whenever the benefit of increased protection against herbivores exceeds their cost. The Resource Availability Hypothesis further predicts that the quantity and type of defenses produced by plants will depend on the availability of the resources. According to RAH, fast growing trees will invest in the cheapest type of defense (favor growth) while slow growing trees would benefit from investments in more expensive defense strategies (favor defense).

As compared to RAH, which focuses on the evolutionary nature of resource allocation by plant species, Carbon-Nutrient Balance theory (CNB) is concerned with how the environment influences the phenotypic expression of chemical defenses. The basic premise of CNB is that nutrient deficiencies limit growth more than the rate of photosynthesis. Plants experiencing nutrient deficits are expected to decrease growth yet continue to photosynthesize, though at a lower rate. Any excess carbon from photosynthesis would be available for production of carbon-based defenses (e.g. terpenes and phenolics). When the carbon:nutrient ratio is reduced, due to diminished light for instance, production of carbon based defenses would be reduced. However, changes in terpene levels in conifers often do not conform to this hypothesis.

The failure of the CNB model to reliably predict the responses of carbon-based defenses to alterations in light and nutrient supply may be related to its basic assumptions. For example, the assumption that production of carbon-based compounds is not costly to plants fails to take into account the significant biosynthetic, storage, and maintenance costs. Construction of biosynthetic enzymes and multicellular storage structures requires adequate supplies of nutrients (e.g., nitrogen, sulfur, phosphorus). Thus, accumulation may proceed only at a limited rate under conditions of nutrient scarcity, regardless of the availability of photosynthetic carbon. The Carbon-Nutrient Balance theory also assumes that manufacture

of carbon-based defenses is influenced chiefly by changes in the supply of carbohydrates. However, the amount of carbohydrates available are just one of many factors (e.g., gene expression, enzyme availability) regulating biosynthesis.

The Growth-Differentiation Hypothesis (GDH) was originally proposed as a strategy for plant growth. Many years later, the theory was applied to plant defense. The Growth-Differentiation Hypothesis expresses a genetic trade-off between a plant's investment in growth and defense. The theory divides development into two distinct processes: growth, which includes cell division and enlargement, and differentiation, which includes cell maturation, specialization, and the production of defensive compounds. According to GDH, as resources are limited cell growth is limited more than differentiation. The theory also asserts that resource supply controls the distribution of defenses in plants by invoking shifts in development. As with CNB, declines in resources are believed to inhibit growth before they affect photosynthesis. Conversely, photosynthesis is expected to continue under adverse environmental conditions, leading to a build-up of carbon that serves as a source of raw materials for differentiation. It is subject to the same inadequacies as CNB.

These theories are among the most commonly tested in the field of plant defense. The staggering number of studies refuting them has led many to believe that development of an all-encompassing defense theory may not be a realistic expectation. One shortfall shared by many of these theories is employment of growth as the currency against which defense is measured. While growth is convenient to measure, it may not adequately reflect the proper metric, i.e. plant fitness. A better understanding of plant defense may come from incorporating life-history traits in future theories.

Current plant defense theories also emphasize the idea that plants evolve defenses in response to attack by herbivores, while herbivores meet the challenge by evolving detoxification systems (i.e., reciprocal coevolution). However, recent research indicates that reciprocal coevolution is restricted to herbaceous plants and specialized insects. On the contrary, many invertebrate and most vertebrate herbivores are generalists that eat a variety of foods. Thus, evolutionary interactions have been diffuse rather than reciprocal for the majority of herbivores and plants and should be considered as such in plant defense theories.

If current plant defense theories fail to adequately predict the distribution and allocation of plant defenses, what value do they offer? Taken together, they offer these important concepts that must be considered in plant-animal interactions: 1) plant defenses are genetic traits shaped by evolution and passed on to future generations; 2) plant defenses are metabolically costly; 3) the quantity and distribution of plant defenses are dynamic and influenced by both the abiotic and biotic environment.

4. Mammalian Metabolism of Phytochemicals



When a mammal eats a plant, both beneficial and deleterious phytochemicals are ingested. The types and amounts of phytochemicals ingested are ever-changing due to abiotic factors and the variety of plant and animal populations interacting with these same plants. Mammals have themselves responded to the phytochemical diversity they encounter. They are equipped with metabolic pathways that have evolved in the face of this dynamic system.

4.1. Digestion and Oxidation

Mammals expend energy in diverse ways, including basal metabolism, activity, thermoregulation, and reproduction. To meet these needs, digestion and metabolism combine to release energy from ingested foods. Digestion produces simple sugars from complex carbohydrates, free fatty acids from lipids, and amino acids from proteins. These digestive end products are then converted to energy in the cells by a series of key biochemical cycles known as the final oxidative pathways.

In ruminants, microbial fermentation of carbohydrates produces volatile fatty acids that enter directly into the oxidative processes to yield energy. Fermentation is also responsible for digesting cell wall carbohydrates that are not otherwise metabolized by monogastric species. Amino acids may also be produced in the forestomach via fermentation. The amino acids produced by hydrolysis of proteins and peptides can be incorporated into new proteins (e.g. muscle mass, enzymes) or deaminated and oxidized to yield energy.

Without the aid of microbial fermentation, monogastric herbivores rely on enzymes present in saliva, gastric juice, pancreatic secretions, and intestinal juice to produce simple sugars, free fatty acids, and amino acids from the foods they eat. Absorption of these digestive products occurs mostly in the large intestine, making them available for the oxidative pathways in the cells.

4.2. Detoxification

Mammalian herbivores are also equipped with a series of biochemical pathways designed to process secondary plant compounds. Mammalian detoxification involves three steps: primary metabolism, conjugation, and elimination. Deleterious plant compounds are transformed into more polar compounds by primary metabolism and conjugation. Primary metabolism, or Phase I biotransformation, involves enzymatic oxidation, reduction, or hydrolysis. Elimination of the toxin is enhanced because the non-polar, foreign species is covalently bonded to a polar, endogenous compound. Conjugation, or Phase II biotransformation of plant defensive compounds, principally results in the formation of toxin-glucuronic acid conjugation products that are eliminated in feces and urine.

Detoxification allows herbivores to make use of plant nutrients while circumventing the plants defensive arsenal. However, detoxification reactions proceed at finite rates. When the rate of toxin absorption exceeds the rate of detoxification, toxins accumulate in bodily tissues and toxic effects are observed. Though detoxification effectively eliminates toxins from the body, it is a costly biochemical process. Production of glucuronic acid from glucose comes at the expense of daily energy requirements. Maintaining acid-base homeostasis also has a significant metabolic cost because production of buffering bicarbonate is achieved via protein catabolism. Thus, nutritional status significantly impacts the ability of an herbivore to tolerate toxins.

The intake of energy and protein is influenced by exposure to defensive compounds and vice-versa. These relationships among nutrients and toxins present in foods vary on a case-by-case basis depending on plant phytochemistry, the experience of the herbivore, and the nutritive state of the mammal. Thus, an herbivore with an adequate basal source of energy

and protein may be more likely to eat a food high in defensive compounds. Conversely, an herbivore that has consumed a food high in toxins may seek complimentary foods high in proteins and energy.

The current understanding of how nutrients influence the kinetics of detoxification processes is incomplete. Where it has been possible to make these assessments, the costs have been substantial and the rate at which toxin-containing foods could be eaten depended on how quickly toxins were detoxified and eliminated from the body.

5. Mammalian Herbivory



Mammalian herbivores must adapt to an ever-changing phytochemical landscape. The quantity and distribution of plant nutrients and toxins change over time and space across a landscape and within an individual plant. Plant phytochemical diversity is shaped by genetics, abiotic conditions, and interactions with herbivores and competing plants. Herbivores must apply their knowledge of the phytochemical environment to meet nutritional needs and avoid toxicosis. This knowledge is shaped by their own morphological and physiological constraints, the inputs of mother and conspecifics, their own experiences, their own nutritional status, and the choices of foods available to them.

Herbivores select or reject particular foods as a result of integration of their experiences with a food and the feedbacks that result from ingestion. Learning permits herbivores to regulate intake in accordance with the concentrations of nutrients and toxins in different foods that comprise the diet. Herbivores can ill afford to reject chemically defended plants outright. Even the most toxic plants contain nutritious primary metabolites. Likewise, even the most nutritious plants may contain some level of defenses. Thus, diet selection is not a yes or no proposition. Rather it is a continuum of intake and feedbacks.

As with any animal behavior, mammalian herbivory is extremely complex. This complexity is illustrated by the variety of disciplines that participate in its examination. Ecologists, behaviorists, psychologists, and animal scientists (among others) bring their own paradigms and terminologies to bear on the subject. Unfortunately, the theories and tenets employed in these fields are not entirely complimentary. The result of integration of these concepts is frequently confusing and frustrating. The discussion that follows does not attempt to reconcile these issues. Rather, it emphasizes the role of consequences in mammalian foraging with terminology intended to avoid conflict with existing paradigms.

5.1. The Genome

Evolution has endowed herbivores with anatomical and physiological adaptations that influence which plants are most suitable for foraging, at what rate plant parts can be ingested, how much can be eaten, and how often. The size and shape of the mouth, teeth, the structure of its digestive system, liver and other organs, as well as visual acuity, and basal metabolic rate are examples of intrinsic properties granted mammals by their parents and generations of natural selection. Mammals are further endowed with a neural system that links the mammals internal environment, from mouth to gut to brain. The nervous system integrates internal (morphology and physiology) and external (social and physical)

environments.

The genome contains the "memory" of evolution. Information contained in the genome has the potential to develop in various ways - neurologically, morphologically, and physiologically - depending on context. Context is provided by micro- (cellular) and macro- (abiotic and biotic) environments. While micro- and macro-environmental experiences during development and early life are especially critical to the individual, genome-environment interactions continue through life and influence future generations.

Behavior is a function of consequences: positive consequences increase, and aversive consequences decrease the likelihood of a behavior recurring. The relationships between consequence and behavior are dynamic and transitory. The environment in which a mammal forages is continually changing, as is the internal environment of the mammal. Consequences are a function of how mammals process sensory information using the tools available to them, i.e. neurologically, morphologically, and physiologically.

The temporal scales of relationships among behavior, consequence, and genome vary. While behavior and consequences interact with the genome on a short-term basis, the genome itself typically changes over a longer time period. Changes in context, for example the availability of alternative foods, alter the expression of the genome-consequence-behavior relationship. Because contexts change continually as systems evolve from moment-to-moment, year-to-year, and eon-to-eon, so too, do genome-consequence-behavior relationships.

5.2 Affective and Cognitive Learning

When a mammal ingests a food, information regarding the flavor of that food and the physiological effects of ingestion are processed. Preferences or aversions for the flavor arise directly from the postingestive consequences that result from ingesting the food. Preferences are formed for foods that produce energy when metabolized or are otherwise beneficial. Conversely, aversions to foods are formed when ingestion of that food has a negative effect on the individual. Preferences and aversions for specific foods arise from affective learning processes (Figure 1). Learning occurs whether the delay between ingestion and consequence is a few seconds or many hours. Affective learning allows the food item to be identified by its flavor when encountered on future occasions. Without this form of associative learning, herbivores would repeatedly eat the same toxic foods and be far-less efficient foragers of quality foods.

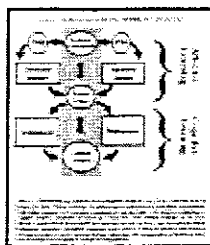


Figure 1. Affective learning integrates the postingestive feedback from eating a food item with the flavor of the food. Plants contribute the phytochemicals responsible for both flavor and feedback. Food intake increases with positive consequences, and decreases with negative consequences. Cognitive learning associates the flavor of a food with other sensory

attributes of the food. Preference and avoidance are mediated by contextual cues such as odor, sight, and location formed by cognitive processes. Individual experience with a food is a result of affective and cognitive processes working in concert. Learning through consequence allows mammalian herbivores to select diets efficiently without having to re-learn the consequences.

Learning via affective processes arises from a sequence of events that begin with the ingestion of a food item. Flavor is the perception that results from the sensory receptors in the mouth and nose to gustatory (sweet, salt, sour, bitter), olfactory (an array of odors), and tactile (astringency, pain) characteristics of the food. At the same time, the sensory receptors interact with visceral receptors that respond to nutrients and toxins, osmolality, and distension during digestion of the food. Primary plant metabolites are oxidized for energy and storage while the secondary plant metabolites are simultaneously detoxified. Within minutes, the effects of ingesting the food are realized. The neurological system integrates signals from sensory and visceral receptors produced by ingestion of the food.

When the net consequences of eating a food are positive (satisfying feedback from needed nutrients like energy and protein), the food is preferred. When the overall consequences are negative (nauseating feedback from toxins), an aversion to the food is formed. Aversions become pronounced when foods contain high levels of toxins or nutrient imbalances. Aversions also result when foods are deficient in nutrients or when amounts of nutrients required for detoxification are inadequate. Collectively, these neurally-mediated flavor-feedback interactions enable mammals to discriminate among foods, each of which possesses a distinct utility, and they encourage mammals to eat a variety of foods and to forage in a variety of locations. The net result is incentive modification when affective learning integrates the flavor of food with postingestive feedback.

The cognitive system integrates other attributes of food with its flavor. Mammals use the senses of smell and sight to differentiate among foods, and to select or avoid foods whose postingestive feedback is either positive or aversive (Figure 1). The net result is behavior modification. In other words, affective processes provide the emotional content of experiences (e.g., like or dislike for particular foods) while cognitive processes render specific details about the context (e.g., where, when, how) in which the experience occurred. Cognitive experiences can be used to learn from mother, from conspecifics, and through trial and error. Together, affective and cognitive processes provide flexibility for mammals to maintain homeostasis as their nutritional needs and environmental conditions change.

5.3 Palatability

An herbivore's internal (experience through learning, nutritional state, etc) and external (social facilitation, choice, etc) environment interacts to define the palatability of specific foods (Figure 2). The palatability of a particular food varies from day to day and can even change over the course of a single meal. Satiety, the decrease in desirability of a particular food due to repeated ingestion, is one example of changing palatability. The satiety hypothesis attributes changes in palatability to transient food aversions due to flavors, nutrients, and toxins interacting along concentration gradients. Gustatory, olfactory, and visual neurons stop responding to the taste, odor, and sight of a particular food eaten to satiety, yet they continue to respond to other foods. Aversions occur even when a food is

nutritionally adequate because appetite is a continuum from hunger to satiety to surfeit. Thus, cyclic patterns of intake of different foods are due to eating any food too often or in too large an amount, and the less adequate a food is relative to a mammals needs, the greater the aversion.

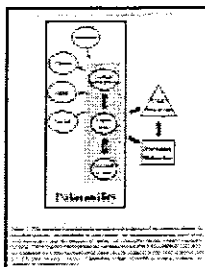


Figure 2. The anatomical, morphological, and physiological features of the herbivore selected by evolution (genome), the availability of foods (choice), the nutritional/reproductive status of the individual (state), and the influence of mother and conspecifics (social) impact associative learning. Taken together, these internal and external processes define the palatability of a food. The palatability of a food has tremendous impact on what an herbivore eats (diet selection) and how it is eaten (foraging behavior). Furthermore, because the system is dynamic, behavior can influence the palatability of a food.

The palatability of a particular food influences foraging behaviors associated with the acquisition of that food (Figure 2). For example, black bears (*Ursus americanus*) learn through feedback from nutrients (affective process) to prefer vascular tissues from conifers in stands of low tree density. Preference for conifers in low-density stands is due to their higher vascular tissue carbohydrate concentration compared with trees in high-density stands. At the same time, low-density tree stands are visually different from high-density stands. Bears learn to visually identify highly palatable trees (cognitive process), precluding the need to taste individual trees first.

In this dynamic system, behavior can also influence palatability. For example, food handling can positively impact palatability of certain foods. Primates have learned to wash foods prior to ingestion. Once learned, this information is passed from generation to generation. Domestic livestock exhibit the same kinds of cultural transfer of learned foraging behaviors. Early human history is rife with examples of manipulating food palatability via leaching and heating. Caching food is another behavior that impacts palatability by causing the concentrations of some secondary metabolites to decrease during storage. Further, presence of plants containing high-levels of phenolics in the cache assists in preserving the contents during storage.

Geophagy is another foraging behavior that could have arisen from learning through consequences. Soil consumption influences palatability by binding plant defensive compounds and promoting rapid excretion. Toxin binding has been implicated as the motivation behind geophagic behavior of elephants, macaques, mountain gorilla, and humans.

5.4. Social Learning

Mother and peers have immense influence on the foraging behavior of individuals. Young mammals learn what and what not to eat and where and where not to go from interactions with mother and peers. Social interactions enable offspring to quickly learn to identify nutritious foods and to avoid those that are toxic. In the process of foraging with mother, young mammals learn to discriminate the foods mother eats: from familiar foods, to foods mother avoids, to novel foods. Offspring are not likely to ingest foods rejected by mother and prefer those foods that mother ingests. Chemical information regarding which foods mother is eating can even be passed to her offspring in-utero and in milk. Nutrients, toxins, and flavor components of foods ingested by mother are passed through the placenta, allowing fetuses to learn about foods simultaneously with mother (similarly mediated by affective learning). Likewise, phytochemicals from mother's diet can also be transmitted to her offspring during lactation through mother's milk.

Mammals are wary of the unfamiliar, including unusual foods, places, and individuals of the same or different species. Social learning is an efficient mechanism for overcoming neophobia. Mother and/or conspecifics can identify which foods, novel to the individual, are safe and which are toxic. However, individual experiences still play a major role in diet selection. If the consequences of ingestion are positive, mammals gradually increase intake of the novel food until it becomes a part of the diet. If the consequences are negative, herbivores limit intake of the novel food in accordance with the concentrations of the toxins in the food. In general, social influences may be important to introduce patterns of behavior, while individual experiences dictate if the preference or aversion should be maintained.

Social learning is not limited to mother-offspring interactions. The presence of a conspecific near food increases the likelihood that others will eat food located there. Individuals (observers) may also learn of the consequences of a particular food by watching the behavior of conspecifics that consume the item (demonstrators).

5.5 Nutritive State

There has been a long-standing debate over the ability of mammals to balance their diets nutritionally. Some contend herbivores are unable to prevent nutrient imbalances; others claim they innately recognize nutrients in foods. There is little evidence to support either position. However, there is ample evidence that animals forage to correct nutritional imbalances both deficits and excesses.

Animals acquire aversions to nutrient-deficient foods. Reduced preference for a familiar diet depends on the severity of the deficiency. Aversions cause animals to sample novel foods. If the consequences of eating the novel foods are positive - they help to rectify the deficit - animals acquire preferences for the new foods. The sequence of aversion-sample-preference enables animals to maintain nutrient balance.

Mineral imbalances commonly cause food aversions in domestic ruminants. Phosphorus deficiency in cattle, sheep, and goats depresses intake by 10 to 50%. Lambs deficient in essential amino acids acquire strong aversions to the food(s) they were eating during the deficiency and acquire preferences for foods that rectify the deficits. The onset and strength of the aversion depends on the severity of the deficiency. Excesses of minerals also cause food aversions. Intake increases as mineral concentrations increase or as electrolyte balance

improves, but intake declines as concentrations increase beyond needs or as balance changes.

Preferences for macronutrients are also a function of the nutritional state of the herbivore. Preference for food high in energy increases after a meal high in protein (likewise, preference for protein increases following a meal high in energy). The balance of energy and protein affects the rates of production of end products of fermentation such as organic acids and ammonia. The rate at which energy and protein are released cannot exceed the rate at which they can be processed without causing excesses. As with micronutrients, excess production of organic acids or ammonia will produce aversions to the foods that metabolically yield these end products.

5.6. The Power of Choice

The availability of food choices profoundly affects diet selection. Total intake of a single food item can increase simply by offering multiple choices of that same food item. This is sometimes termed the "variety effect". At the same time, preferences among different foods are influenced by palatability.

When a variety of foods are available, herbivores can afford to avoid a particular food item that produces negative consequences - even if the alternatives are not as nutritious as the food being avoided. Thus, the persistence of a food aversion can be prolonged when alternative foods are present. Conversely, when there are no choices herbivores eat toxic foods - despite the negative consequences.

Eating a varied diet may permit mammals to "spread the risk" of toxicosis. Herbivores can increase overall intake of toxic foods when presented with a variety of foods containing different toxins. Higher overall doses of defensive compounds can be ingested when individual toxins act on different organs or are detoxified by different metabolic pathways. In other words, negative feedbacks are reduced when complimentary toxins are ingested. Similarly preferences occur when diet mixing enables an herbivore to meet its nutritional goals for both macro- and micronutrients.

5.6 When Learning Fails

Though mammals can learn to select nutritious foods and minimize over-ingestion of toxins, on occasion they die from eating toxic plants. This occurs most commonly when herbivores exceed the capacity of the landscape. With domestic mammals, this may occur when pasturelands are overstocked. With wild herbivores, this occurs when populations exceed carrying capacity.

While lack of alternative foods may cause this, herbivores will eat toxic plants even in the presence of highly nutritious foods. This occurs when learning processes fail. For instance, herbivores in unfamiliar environments often suffer from malnutrition and ingest toxic plants as they attempt to learn what and what not to eat. Moreover, the same dose of a toxin can have a much greater effect in an unfamiliar than in a familiar environment. Delayed feedback also diminishes aversions to toxic foods. For example, larkspur (*Delphinium spp*) is over-ingested by cattle, in part, because positive feedbacks occur more rapidly than the

negative consequences of ingesting the toxic alkaloids present in the plant. The delay between ingestion and negative postingestive feedback can have durations of several days, months, or even years with some toxins.

Related Chapters



Related Links will be activated soon!

Glossary



Carbon-Nutrient Balance Theory (CNB): A plant defense theory that suggests individual production of defensive compounds is influenced by the availability of resources such as water, nutrients and light.

Detoxification: The physiological and metabolic processes of herbivores that allow for the transformation and elimination of toxins.

Flavor Aversion Learning (FAL): The acquired aversion to a particular food resulting from experience with that food.

Generalist: An herbivore that forages on a variety of plant species.

Growth-Differentiation Hypothesis (GDH): A plant defense theory that suggests individual production of defensive compounds is influenced by tradeoffs between plant growth and differentiation. As with the carbon-nutrient balance hypothesis, declines in resource availability are believed to inhibit growth before they affect photosynthesis.

Optimal Defense Theory (ODT): A plant defense theory that suggests plants allocate defenses in a manner that maximizes individual fitness. The theory is concerned with tradeoffs between costs and benefits of allocating resources to defense and growth.

Oxidative Pathways: The metabolic processes of mammals that produce energy from primary plant metabolites.

Phytochemical: Chemicals of plant origin.

Primary Metabolites: The universal constituents of plant cells and tissues, such as simple carbohydrates, starches, lipids, and proteins.

Resource Availability Hypothesis (RAH): A plant defense theory stating that evolutionary trade-offs between growth and defense are influenced by available resources.

Secondary Metabolites: Phytochemicals produced by plants that defend tissues against herbivores, pathogens, and competing plants.

Specialist: An herbivore that forages exclusively on a particular plant species.

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Biographical Sketches



Bruce Kimball is a research chemist with the USDA National Wildlife Research Center (NWRC). The mission of the NWRC is to develop new tools to solve wildlife-human conflicts. Bruce received his M.S. (Analytical Chemistry) from Arizona State University and his Ph.D. (Ecology) from Colorado State University. His primary research focuses on chemically mediated behaviors in mammalian wildlife. This includes investigating chemical constituents present in natural systems and examining relationships between phytochemistry and wildlife use of agricultural resources. His research is conducted in the field, with captive animals, and in the chemistry laboratory.

Fred Provenza's research focuses on understanding behavioral principles and processes and using that understanding to inform management. For the past two decades, his research team has studied the role of learning in food and habitat selection by herbivores. He has co-authored 115 papers in peer-reviewed journals and his group has been asked to co-author an additional 51 synthesis papers for peer-reviewed journals, books, and proceedings. In 1999, he received the W.R. Chapline Research Award from The Society for Range Management for exceptional research accomplishments that enhance management of landscapes. This award is given annually to the person whose research most embodies excellence in Range Science. In 1999, he also received the University Outstanding Graduate Mentor award from Utah State University. He has supervised 45 graduate - M.S. and Ph.D. students and post-doctoral students from 19 different countries.

EOLSS - CHEMICAL DEFENSE AND MAMMALIAN HERBIVORES

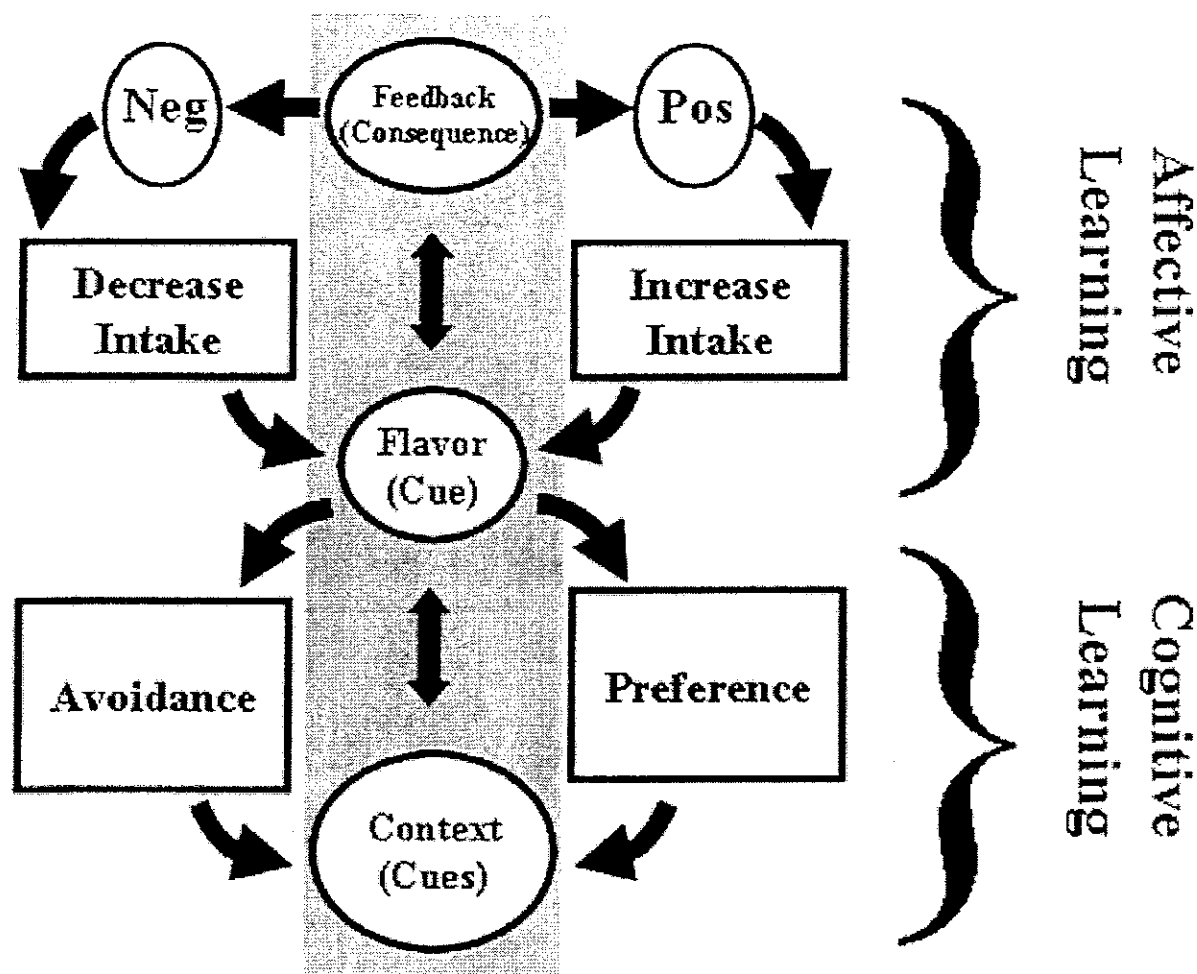


Figure 1. Affective learning integrates the postingestive feedback from eating a food item with the flavor of the food. Plants contribute the phytochemicals responsible for both flavor and feedback. Food intake increases with positive consequences, and decreases with negative consequences. Cognitive learning associates the flavor of a food with other sensory attributes of the food. Preference and avoidance are mediated by contextual cues such as odor, sight, and location formed by cognitive processes. Individual experience with a food is a result of affective and cognitive processes working in concert. Learning through consequence allows mammalian herbivores to select diets efficiently without having to re-learn the consequences.

EOLSS - CHEMICAL DEFENSE AND MAMMALIAN HERBIVORES

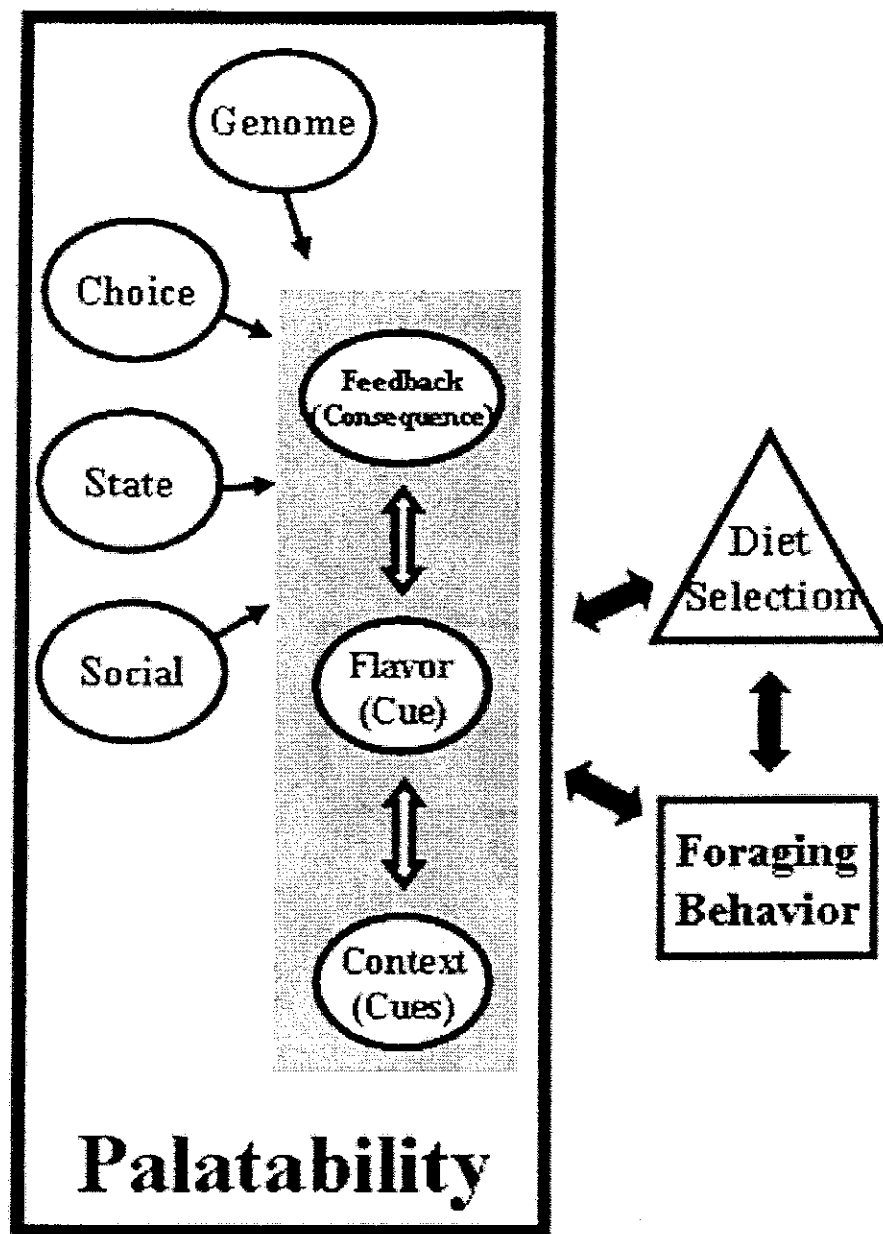


Figure 2. The anatomical, morphological, and physiological features of the herbivore selected by evolution (genome), the availability of foods (choice), the nutritional/reproductive status of the individual (state), and the influence of mother and conspecifics (social) impact associative learning. Taken together, these internal and external processes define the palatability of a food. The palatability of a food has tremendous impact on what an herbivore eats (diet selection) and how it is eaten (foraging behavior). Furthermore, because the system is dynamic, behavior can influence the palatability of a food.